BREEDING AND IMPROVEMENT OF PEAS AND BEANS

B. L. WADE, Senior Geneticist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry

PEAS

NATURALISTS have been interested in *Pisum* for several hundred years, and there are many unmistakable references to peas in the writings of the old Greeks and Romans. Columbus' is reported to have grown peas on Isabella Island in 1493, and General Sullivan destroyed the growing peas of the Indians in western New York in 1779.

Pickering (*50*)[1] states that of the culinary vegetables *Pisum sativum* is the only kind that can with any certainty be traced back to the Stone Age. It was uncommon for peas to be eaten in other ways than as dry, cooked seeds before 1700.

Much of the history of *Pisum* has been well reviewed by Hedrick, Hall, Hawthorn, and Berger (*14*). Ruellius in 1536 was the first to distinguish between garden and field peas. Since *Pisum sativum* L., the garden pea, and *P. arvense* L., the field pea, are completely cross-fertile, the distinction seems entirely artificial, and most writers now consider both types under *P. sativum*. In addition some varieties of garden and canning peas (unquestionably *P. sativum*) are used extensively for field peas.

It is noteworthy that peas were the first crop with which controlled breeding work for the production of new varieties was begun, and also that they were the crop with which Mendel conducted his historic experiments, which were the beginning of the modern science of genetics.

Vavilov (*80*) indicates that peas probably had their origin in Ethiopia, with secondary centers of diversity in Mediterranean Europe and in southwestern and central Asia. Although many forms are known in the Mediterranean region, peas have never been of much importance in that area. Farther north, in England, peas have reached their greatest perfection, and they are an important crop in Scandinavia, Germany, the Netherlands, and France. The Union of Soviet Socialist Republics at the present time probably surpasses all other countries in the production of peas, mostly dry edible seeds. In 1929 the acreage of peas for grain in the Union of Soviet Socialist Republics was 1,435,750 acres. The estimated crop for 1931 was 2,750,000 acres.[2] Further increases are anticipated. The United States pea acreage for all purposes probably does not exceed 1,000,000 acres.

[1] Italic numbers in parentheses refer to Literature Cited, p. 277.
[2] Communication from R. K. Bonnett, Moscow, Idaho, 1931.

The pea is a vegetable easily introduced in most places where the climate is favorable. The plants of many varieties are cold-hardy and will survive a winter under a snow covering. If slightly frozen they will put out new shoots when the weather becomes warmer. The blossoms are not particularly cold-tolerant and will survive only a light frost. Peas do not thrive very well in warm weather, so their culture in the southern and southwestern United States is confined largely to the winter and spring months. In the southern part of the Union of Soviet Socialist Republics, where summer quickly follows winter, peas are grown to a limited extent. In the north-central part of the Union of Soviet Socialist Republics, east of Leningrad, west of Moscow, and in southwestern Siberia they are a very important crop.

Peas may be divided into at least five classes according to use: (1) Forage or green-manure crops, (2) dry, edible seeds, (3) market-garden or green shelling peas, (4) canning peas, and (5) edible-podded peas, which have no lining membrane in the pod, a condition that has been traced to two genes. The Union of Soviet Socialist Republics and the southern United States devote large acreages to forage and green-manure crops. Nearly all the important pea-producing countries devote large areas to the production of seed for food and feedstuffs, especially the Union of Soviet Socialist Republics, Germany, the Netherlands, and the area around Spokane, Wash., in the United States. Classes 1 and 2 above are usually referred to as field peas. California produces more than two-thirds of the market-garden or truck peas grown in the United States, of which the annual acreage is now well over 100,000 acres.

The climate of England is especially favorable to the production of large-podded market-garden peas of high quality.

Lately the preservation of shelled green peas by freezing has become important in some parts of the United States, particularly the Pacific Northwest. This industry uses both market-garden and canning varieties, but several seedsmen are now working to develop varieties especially adapted to freezing.

THE *most highly evolved pea variety so far produced by breeders is probably Laxton's Progress. It has a very dwarf vine with a zigzag stem, which makes it sturdy and upright; dark-green foliage; and large, straight, dark-green, pointed pods, from which the peas can be shelled readily. Each of these characteristics is important to growers and each received attention in breeding. The most notable characteristic of Progress, however, is that it begins to bloom at the eighth or ninth node on the stem. This may not seem significant to the inexperienced, but to pea farmers it is worth years of difficult breeding work; for it means that Progress is a few days ahead of its nearest rival in excellence, Hundredfold, which does not begin to bloom until the ninth or tenth node.*

The United States cans annually from 12,000,000 to 20,000,000 cases of peas,[3] mainly in the States of Wisconsin, New York, Maryland, Michigan, and Washington. The canning of peas is not an extensive industry in any other country at present. Edible-podded peas are widely grown in continental Europe. They are for the most part more tolerant to heat than are other peas and have now become a rather common vegetable in Hawaii and southern China. In the continental United States they are practically limited to home gardens.

Origin of the Older Varieties

Thomas Andrew Knight, of Downton Castle, Wiltshire, England, the first great hybridizer, began his work with peas in 1787. Some of his varieties are still used, and they have been the foundation breeding stock for most modern pea varieties.

In 1822 John Goss published a paper in which he recognized the dominance of yellow cotyledons and that green segregates from his crosses bred true. If he had carried his observations a little farther he would have antedated Mendel's discoveries by some 40 years.

Succeeding Knight, many famous pea breeders began their work in England. About 1860 McLean, of Colchester, produced Little Gem and his important Advancer, from which the American varieties Abundance and Perfection were derived. Thomas Laxton bred the variety that bears his name, introducing it in 1898. Laxton Bros. later produced Laxtonian about 1907, and Progress in 1921.

Culverwell originated Telegraph, a smooth-seeded variety with long pods and a tall vine, some time before 1877. It became very popular both in England and in the United States. Telephone, a wrinkled-seeded strain of Telegraph, was derived from Telegraph by Carter in 1878, and has largely replaced it, probably on account of its much better quality. Alderman, introduced by Laxton about 1891, has largely replaced Telephone in the United States, probably because of the demand for darker pods.

Several English seed companies have for at least 50 years poured a continuous stream of new varieties into the markets of the world. Most of these have been successful only in England, but such a diversity of varieties has been supplied that most countries find themselves using a number of varieties that originated in England. The principal English seed companies contributing to pea improvement have been Laxton Bros., Sutton & Sons, Carter & Co., and Hurst & Co.

All American varieties are undoubtedly similar to English varieties and in many cases confusion exists as to the origin of a given variety. Alaska was introduced as an American variety by A. B. Cleveland about 1880. It is so similar to the English variety Earliest of All, a cross of Ringleader×Little Gem, introduced in 1881 by Laxton, that these two varieties are now indistinguishable. Alaska is a smooth-seeded, very early, straight-stemmed variety with light-green pods and foliage, which typically begins blooming at the eighth node.

Dwarf Telephone as now grown is a midseason variety blooming at about the fourteenth node. The vine is a sturdy dwarf with a zigzag stem, and the pods and foliage are light green. The pods are long and pointed. Introduced in 1888, the variety is now inextricably

[3] A case equals 2 dozen 20-ounce cans.

mixed and apparently synonymous with Daisy, although originally different. It originated in the United States as a cross of Stratagem × Telephone, while Daisy had its origin in England as a cross of Stratagem and an unnamed variety. Daisy was introduced by Carter about 1891.

Potlatch (Leonard, 1906) is now synonymous with Stratagem (Carter, 1879). These are essentially the same as Dwarf Telephone except that they both have dark-green pods and foliage.

Current Important Varieties

The advent of the canning industry in the United States about 1850, and technical improvements in canning machinery about 1890, gave a great impetus to American pea breeding, and at present the United States produces about as many varieties as are imported from England. The practice of renaming makes it difficult in many cases to be certain of the origin of a variety, since a single name may serve for several closely related varieties, or a single variety may have many names.

The peas with which Knight began his work were smooth-seeded, mostly tall (though a few were dwarf), late, and small podded. The records do not show how he obtained his first wrinkled strain, but he combined the wrinkled characteristic with somewhat larger pods. The quality of sweetness brought in by the wrinkled characteristic soon made his varieties popular, not only in England but in continental Europe.

The English breeders have given but scant attention to disease resistance, but they have gone ahead vigorously to produce larger pods, higher yields, better quality, earlier strains, and sturdier types of vines.

When the early pea breeders began their work, they were interested in dual-purpose peas, that is, peas that could be used in the green-shell condition and also dry. As peas became a more popular vegetable more emphasis was placed on desirable characteristics for a green shelling pea until varieties were developed solely for that purpose. In the early days peas for porridge were cooked whole and consequently both smooth and wrinkled peas could be used. At the present time most dry peas for cooking purposes are sold in a hulled, split condition. As wrinkled peas split with difficulty and it is extremely difficult to remove the hulls, they are no longer produced commercially for cooking in the ripe, shelled condition.

The most highly evolved pea variety so far produced is probably Progress (Laxton Bros., 1921). It has a very dwarf vine, with a zigzag stem—that is, the nodes are not straight but are set at compensating angles so that a very sturdy, upright plant is produced—the pods and foliage are very dark green, and the pods are very large and straight with pointed ends. Progress begins to bloom at the eighth or ninth node and Hundredfold at the ninth or tenth. To the inexperienced there may be no essential difference between Hundredfold and Progress, but to the plant breeder and pea farmers it is worth years of difficult breeding work to have a variety that is a few days earlier than Hundredfold and with pods slightly larger than some strains of Hundredfold. Many peas that have competed with Hundredfold and Progress—such as Blue Bantam (Burpee, 1912), Peter Pan (Watkins and Simpson, 1910), and Laxtonian (Laxton

Bros., 1907)—have failed because of their light-green pod color, slightly smaller pod size, slight pod curvature, tightness of peas in the pod, or some other slight difference of commercial importance.

Before the advent of large-scale shipping of market-garden peas there was no particular reason why varieties with dark-green pods should be preferred to light. However, retail customers began to believe that the light-green pod color was associated either with over-ripeness or staleness of the product, so that today no popular market-garden variety has a light-green pod.

This brings us to the questions of synonyms and misnaming. If a seedsman had a good trade in Laxtonian he might not object to selling Progress or Hundredfold to his customers as Dark-Podded Laxtonian, especially if his customers inquired whether he could not furnish them with a dark-podded strain. After a few years the dark-podded designation might be dropped and the new variety sold under the old name of Laxtonian. As a matter of fact, in 1928 nearly all strains of Laxtonian had light-green pods, while of the strains examined in 1935 all had dark-green pods except one. Most of the Laxtonian sold in 1935 appeared to be the Hundredfold of 1928, whereas the Hundredfold of 1935 is an improvement over the original strain, with pods that under the best of conditions may be larger than those of Progress.

This process has probably been repeated in practically all groups. In the midseason group (late varieties of peas are not grown in the United States) Daisy and Dwarf Telephone were at first hopelessly confused and then reduced to minor importance in competition with dark-podded Stratagem and Giant Stride. In some places considerable quantities of Dark-Podded Dwarf Telephone are sold, but the variety is in reality only a strain of Stratagem. Giant Stride is a Stratagem type, excellent for shipping on account of its very heavy pod walls.

Canning Varieties

The canning of peas did not attain much popularity in this country until around 1900. There were no canning varieties, and canners tried various market-garden types. They found that they needed characteristics in their canning varieties that market gardeners would find disadvantageous. For instance, they wanted peas with a maximum number of seeds in the edible condition at one time, while the market gardener desired his varieties to produce over a longer period.

In the canning varieties very large pods have been purposely avoided, since they are not particularly well adapted to "vining" machinery, and the yield of shelled peas per acre from large-podded varieties is usually considerably less than from small-podded varieties of the same time of maturity. The early varieties of canning peas all have straight stems with relatively long internodes. This makes them convenient to harvest on poor soils, since early peas with zigzag stems would not make growth enough to be handled efficiently by machinery. Alaska and Surprise are typical of this group and both begin to bloom at the eighth or ninth node. The small pods crack open readily under the impact of the beaters of the pea viner.

The later canning varieties all have zigzag stems except the Admirals, and the pods are usually borne in pairs, although under adverse environmental conditions single pods may be produced. Perfection blooms typically at the fourteenth node. It deviates slightly from Advancer in shape of pod apex and yield, and slightly from Abundance in tightness of pod and node of bloom. Practically all canning peas have light-green pods and seeds, in contrast to the successful market-garden varieties. In an attempt at competition with the market-garden and frozen peas, some canners have canned varieties with dark-green seeds.

The group of peas usually known as Gem has furnished practically all our canning peas. At the time canning became popular, various Gem types were losing their popularity in competition with large-podded market-garden varieties. Canners found, however, that the Gem types that shelled with some difficulty by hand could be shelled easily by machinery and that the yield per acre would be larger than for large-podded peas. The Gem group might be characterized as having on various types of vines, blunt or nearly blunt, well-filled pods of small to medium size, not exceeding 3½ inches in length. From this group, light-green varieties with good to high productiveness, poor to high culinary quality, and early to midseason maturity were selected or bred for canning purposes. There is no popular canning pea with a pointed pod, although many such varieties have been introduced.

Alaska is a smooth-seeded pea with some of the quality of Little Gem, although this quality is not evident in the larger siftings or older seeds from this variety. Alaska retains its prominence largely because of its hardiness under adverse conditions, and the canned product is popular in restaurants, where a fairly tough product is desired that will stand up well after reheating.

Advancer was developed by McLean about 1860 as a market-garden variety. It was from a cross of Beck Gem with some other wrinkled variety. Perfection is of better quality than Advancer and is derived from it by selection. Practically all strains now offered as Advancer are in reality Perfection. Differences in Perfection and Advancer are difficult to state exactly, but in general the Perfection pods are slightly larger and the yield is somewhat greater under comparable conditions. Perfection, and improvements from it, now constitutes the most important midseason canning pea variety.

Surprise (Horsford, 1889), from a cross of Earliest of All × American Wonder, is one of the best-quality peas known. It is in season with Alaska and before maturity can be distinguished from Alaska only with difficulty. The major difference seems to be a greater amount of marbling on the stipules of Surprise.

Prince of Wales is a large-seeded Gem type, somewhat later in season than Perfection, but even under the best of conditions the pods do not fill well. It is popular in limited areas for the canning of peas ungraded as to size, of a darker green color than Perfection.

Many seed companies are now attempting to develop pea varieties especially adapted to preservation by freezing. Perhaps the ideal freezing varieties will have relatively large seeds and medium-sized pods that can be handled by the vining machinery now used for canning varieties. To be successful as a variety for freezing, the seed color must be dark green without developing a bronze tone when the pack has been thawed.

Summary of Varieties

A summary of the principal varieties in common use at the present time includes—

Canning peas:
- Alaska
- Perfection
- Surprise
- Prince of Wales
- Green Admiral
- Yellow Admiral

Market-garden peas:
- Progress
- Hundredfold
- Giant Stride
- Alderman
- World Record
- Gradus

Market-garden peas—Continued.
- Thomas Laxton
- Early Gilbo
- Dwarf Telephone
- Stratagem

Field peas (dry edible and cover-crop groups):
- Alaska
- Blue Bell
- First and Best
- Extra Early
- White Canada
- Austrian Winter

Of the six canning varieties listed, only two are of undoubted English origin—Prince of Wales (Green Giant) and Yellow Admiral (Fairbeard Nonpareil)—and both are of minor importance. Green Admiral, also of minor importance, was derived by selection by Rogers from Yellow Admiral. Alaska has been subjected to intensive breeding work by Delwiche, Renard, Rieman, Wade, and Temple, especially for resistance to fusarium wilt. Perfection (Gallatin Valley Seed Co., 1914), derived from Advancer, has been the subject of much breeding work for wilt resistance by Renard, Delwiche, and Wade. New wilt-resistant Surprise types, derived from crosses of Surprise × Alaska or Surprise × Peerless, have been bred by Delwiche, Wade, and Renard.

Of the market-garden types none is of undoubted American origin except Early Gilbo (Rogers, about 1934). The three of greatest importance are unquestionably of English origin. The greatest contribution of American seedsmen to the English market-garden varieties lies in their selection of pure lines in which the incidence of "rabbit ear" and other rogues is very low. Rabbit ear is a condition in which the leaves, stipules, and pods are greatly reduced in width while retaining approximately the same length, so that at a distance the stipules look like the ears of a cottontail rabbit.

In the field-pea group Alaska is again first. Blue Bell, which probably originated in continental Europe, had its name changed from Blue Prussian during the World War. First and Best and Extra Early are of American origin. White Canada and Austrian Winter are probably from the countries indicated by the names. Little effort has been expended in developing varieties suitable for field peas. The University of Idaho strain of Blue Bell, named Idabell, is a superior strain of that variety. Some seed companies that grow a great many field peas possess pure lines that, in their freeedom from offtypes, are equal to some of the best strains of canning peas.

Origin and Evaluation of New Varieties and Strains

The Wisconsin Agricultural Experiment Station group working with canning peas have greatly influenced the trend in the industry. E. J. Delwiche has been prominent in this work and has contributed at least 11 strains, of which Badger (1921), a variety like Perfection, was the first introduction. Badger is of exceptionally high quality, but the canning trend away from small seeds and susceptibility to wilt has prevented its general use. Horal (1923), a small-vined Perfection type, one of the heaviest-yielding peas known to the canning industry, failed to achieve popularity because of its very decided lack of quality coupled with small seed size. Alcross and No. 19 strains of Alaska have been of value in breeding homozygous wilt-resistant strains of Alaska peas. They are still grown to a considerable extent, and some of the completely wilt-resistant strains of Alaska on the market have been selected from them. Ashford (1924) is an exceptionally good strain of Horsford, but it is later than Perfection, and therefore the demand for it is very limited. Wisconsin Early Sweet (1931) is a vigorous wilt-resistant type approaching Surprise in quality and having the hardiness of Alaska. It promises to become a very important variety. Wisconsin Perfection (1933) has achieved some popularity on account of its hardiness and wilt resistance.

The Canners Seed Corporation has introduced several new strains of peas since 1930. These have all resulted from the breeding work of E. J. Renard. All introductions by this company have been pure (homozygous) for wilt resistance and were bred especially for adaptation to conditions in Wisconsin. Wilt-resistant Perfection (1930), wilt-resistant Alaska (1930), and wilt-resistant Early Perfection (1933) have been very favorably received by the canning trade. The popularity of large-seeded Perfection and Improved Wales will depend on the trend of the canning industry toward or away from large-seeded types.

The Washburn-Wilson Seed Co. has introduced several strains of completely wilt-resistant peas since 1932. These are for the most part the result of breeding work carried on by the writer. The most successful of these seem to be Walah (1932), from Prince of Wales; Alah (1932), which is a wilt-resistant Alaska; and Mardelah (1935), a wilt-resistant Surprise type.

C. E. Temple, of the Maryland Agricultural Experiment Station, has originated a strain of Alaska that does well under conditions existing in Maryland and adjoining States. It is resistant to fusarium wilt (caused by *Fusarium orthoceras* Appel and Wr. var. *pisi* Linford) and possibly to certain other diseases.

Stuart F. Smith, of the Sioux City Seed Co., has produced wilt-resistant strains similar to Alaska and Perfection. M. C. Parker, of the Gallatin Valley Seed Co., is breeding peas for fusarium wilt resistance, types for freezing, and types with multiple pods.

It would appear from the emphasis on wilt resistance that fusarium wilt has been of great importance in the United States. To a considerable extent it has been important, even the limiting factor in certain areas. Probably the most interesting thing in connection with the work on fusarium wilt has been the general adoption of pure-line breeding by the seed companies. It was found that most stocks of partially wilt-resistant strains did not give good canning results, on account of the mixture of prematurely ripened peas from susceptible plants with the normal peas from the resistant plants. After it was found that pure lines were highly satisfactory in the wilt work, pure-line methods were used in connection with other seed stocks, so that the standards of the industry with regard to rogues have been very definitely raised.

Much confusion usually exists in the seed industry as to the exact identity of strains. It is not improbable that some one strain of wilt-resistant Alaska or other varieties may come to be considered of outstanding merit. However, with the lapse of time and the tendency to substitute similar things for each other, confusion will arise as to the actual strain employed. Many companies have found that wilt-resistant Alaska and wilt-resistant Perfection are entirely satisfactory as canning peas and cannot be distinguished in any definite way from corresponding susceptible biotypes except in reaction to wilt, so that they feel justified in carrying only one strain of each major variety. New York State apparently does not have a wilt problem, but many of the Alaska and Perfection stocks delivered in that State are wilt-resistant.

The future canning types for this country are rather unpredictable, but it seems likely that early peas with stems like Alaska or Surprise, and later peas with heavier stems like Perfection, will be in demand. Large-seeded strains are being sought for the canning of ungraded "sweets", but so far they have not given entirely satisfactory yields. Resistance to diseases other than wilt, to insects, and to adverse weather conditions all are problems that will be worked on in the near future by plant breeders, and in some cases such work is already under way. Searles, at the Wisconsin Agricultural Experiment Station, is doing some work on tolerance of pea varieties to aphid injuries.

Among the market-garden types, Progress (Laxton Bros., 1921) is the most important variety. Hundredfold (Sutton, 1910) is next in importance. These two varieties have largely replaced similar varieties like Laxtonian, Blue Bantam, Pioneer, and Peter Pan. Giant Stride (Carter, 1916) is now probably third in importance. It has largely replaced Dwarf Telephone and Stratagem in the western United States. As introduced it was quite a variable strain. Asgrow No. 40 and Stridah are pure-line selections from Giant Stride or similar material introduced in 1930 and 1931. Recently the United States Department of Agriculture, partly in cooperation with the California Agricultural Experiment Station, has proceeded with crosses between Giant Stride and Progress in which desirable early Progress and Hundredfold types have been selected for resistance to strains of *Fusarium*.

Seed stocks handled under the name of Alderman consist essentially of two types. One type is true Alderman (Laxton, about 1891) and is extensively grown in home gardens where a variety adapted to trellising is desired, and to a limited extent in commercial market-garden areas. The other type is common in the truck-farming areas of the West and is either Quite Content (Carter, 1906) or a derivation from a cross of Alderman with Quite Content. The largest pods and most fancy packs of market peas obtained in the United States are made from this second type of Alderman, which really deserves a name of its own. Sometimes it is referred to as long-pod Alderman, or Alderman with some geographic designation. The best way of differentiating between the Alderman types is by noting pod-wall thickness. The old type of Alderman has a thin pod wall and the new type has a much thicker pod wall.

Early Gilbo (Rogers, about 1934) is an exceptionally promising variety midway in season between Hundredfold and Giant Stride. The pods are straight, well-filled, approximately as large as those of Giant Stride, and moderately thick walled.

Gradus, Thomas Laxton, and World Record are popular in certain areas in the eastern United States, but the pods are so small that western shippers do not use them. These are all early, straight-stemmed varieties blooming at the eighth to tenth nodes. Thomas Laxton has blunt pods, the other two have pointed pods.

Many American seed companies have contributed to the introduction or breeding of superior varieties and strains of peas. Among these should be mentioned Associated Seed Growers, Inc., and their predecessor firms, the Everett B. Clark Seed Co., the John H. Allan Seed Co., and N. B. Keeney & Sons; the Ferry-Morse Seed Co. and their predecessor firms, D. M. Ferry & Co. and C. C. Morse & Co.; the Rogers Bros. Seed Co.; the Washburn-Wilson Seed Co.; the Gallatin Valley Seed Co. and its predecessor firm, the Davis Seed Co.; the Canners Seed Corporation; the Sioux City Seed Co.; W. Atlee Burpee & Co.; the Jerome B. Rice Seed Co.; Francis C. Stokes & Co. and their predecessor firms; the Chas. H. Lilly Co.; the Livingston Seed Co., and Vaughn's Seed Store.

SNAP BEANS

History and Use

Beans (*Phaseolus vulgaris* L.) were introduced from the Americas to Europe and Asia, where they early became popular. They were mentioned in Europe about 1542, and by 1616 a large number of varieties of different types were described. Hedrick, Tapley, Van Eseltine, and Enzie (*15*) have given a very satisfactory summary of the early history of beans and descriptions of varieties now grown or once grown in the United States. The most extensive previous studies of bean varieties were made by Irish (*17*), Tracy (*77*), and Jarvis (*18*).

Beans may be divided into three major classes according to form in which they are harvested and used—(1) dry shell, (2) green shell, (3) snap or green beans. There is some overlapping of these groups. For instance, Canadian Wonder is thought of as a dry shell bean in this country but is considered a good snap bean in parts of the British Empire. Low Champion as used falls in all three categories. Snap bean varieties may be further divided into (a) market garden, (b) home garden, and (c) canning beans, but distinctions on such a basis are not particularly valid, since most of the canning beans are frequently used for the other two purposes. Most of the present discussion will be concerned with snap bean varieties and their development.

Beans are also classified according to type of vine and pods. A bush bean is a type in which the inflorescence is at the tip of the plant; when it appears, the plant stops growing. In a pole bean, on the other hand, the flowers are along the stem, which continues to grow indefinitely, its ultimate length depending on environmental conditions. All bean pods are green when they are very small, but some turn white, yellow, or crystal[4] as they approach an edible stage. The latter types are called wax beans. Pole beans are mostly used for home gardens. Wax beans are everywhere less popular than green, but they are used for canning, shipping, and home gardens. Since wax pods readily show spots, there has been some discrimination against them in sections where pod-spotting diseases are common. From a shipper's standpoint beans are also classified as flat or round. Beans heart-shaped or oval in cross section are usually classed with the round group, and any pod with a diameter in one direction less than 80 percent of the diameter at right angles to it is considered flat.

At the present time Florida produces well over half the shipping crop of market-garden snap beans. New York, Maryland, Wisconsin, Michigan, and Colorado produce a large part of the crop for canning.

Origin of the Older Varieties

An interest in early bean varieties with stringless pods gave the initial impetus to American bean breeding about 1890. Previous to that time seed companies had given but scant attention to bean breeding, apparently being content to introduce a selection made by a farmer or a variety that had become common in some farming community. White Kidney (shell), Dutch Caseknife, Lazy Wife (pole), Early Yellow, Six Weeks, and Mohawk go back too far in horticultural history to be traced with any degree of certainty. Wax beans seem to have been introduced from Europe when Algiers (wax pole) was brought to this country, and German Black Wax (bush) was introduced about 1865.

Even after seed companies became interested in improvement work it was confined mostly to selections from existing stocks or to developing progenies from chance crossings. The seedsmen were seeking early varieties with less fiber in the pod walls and a reduction or elimination of strings as well as a certain smoothness of pod, and in some cases they considered an increase in pod size important. However, these seedsmen gave only incidental attention to offtypes appearing in their stocks, and progress was not very rapid.

The most successful of these early plant breeders was Calvin N. Keeney, of Le Roy, N. Y. Among his productions are Pencil Pod Black Wax, Brittle Wax, Rustless Golden Wax, Wardwell Wax, Burpee Stringless Green Pod, Surecrop Stringless Wax, Giant Stringless Green Pod, and one strain of Stringless Green Refugee. These varieties were all stringless and of very high culinary quality when compared with such varieties as Early Six Weeks and Mohawk, and they all became popular in spite of the fact that they were not quite so hardy as the older varieties. Brittle Wax has persisted as the most popular wax for canning, and Stringless Green Refugee is still the most satisfactory type for canning high-quality green beans. Pencil

[4] Crystal is the term used to describe a nearly colorless, rather translucent-appearing pod.

Pod Wax is of very high quality, but the tendency for the pods to curve has kept it from being a popular garden or shipping bean, and the black seed has prevented it from attaining great popularity as a canner. At the time, however, Burpee Stringless Green Pod was sensationally successful and was grown in most home gardens as well as for canning and shipping. The great success of this one variety stimulated Keeney, as well as other breeders, to continue the development of new stringless varieties, while Burpee Stringless Green Pod remained very popular with home and market gardeners, and Giant Stringless Green Pod became the favorite for an early canning variety for packs of cut beans. Part of Keeney's varieties were introduced by the W. Atlee Burpee Co., part by himself. During the last few years the Keeney stocks have been consolidated with those of two other seed companies incidental to the formation of the Associated Seed Growers, Inc.

D. G. Burlingame, of Genesee County, N. Y., introduced Bountiful in 1898. Other early plant breeders were A. N. Jones, of Le Roy, N. Y.; W. H. Grenell, of Pierrepont Manor, N. Y.; and John Kramer, of Doylestown, Pa.

At the present time the most popular flat-podded, early green snap bean for shipping is Bountiful. There is some competition among early round pods, but Black Valentine (Henderson, 1897), New Stringless Green Pod (Associated Seed Growers, Inc., 1930, from Tendergreen, Henderson, 1922), Full Measure (Henderson, 1906), Burpee Stringless Green Pod, and Giant Stringless are the most popular. Red Valentine, a very old bean of uncertain origin, is still used to a small extent. In some sections Stringless Green Refugee (Keeney, 1908) and 1000:1 Refugee (a very old variety) are still used for late shipping beans. The former is also the most important late canning bean where a high quality pack is desired.

Among the wax beans, Hodson Wax (Harvey Seed Co., 1902) is the most popular late shipper. Webber Wax (1913), Sure Crop Wax (Keeney, 1911), and Davis White Wax (Davis, 1895) are popular early flat waxes for shipping. Brittle Wax (or Round Pod Kidney Wax), Improved Kidney Wax (Keeney, 1906), and Pencil Pod Wax (Keeney, 1900) are the most important of the wax beans for canning

Disease as a Factor in Bean Culture

The ravages of diseases early made it necessary for plant breeders to do additional work on the varieties introduced by Keeney and others after 1890. The three most important bean diseases in this country are caused by organisms that invade the seed tissues, remain dormant in them, start new outbreaks on the seedling plants, and cause losses later. These diseases are anthracnose, bacterial blight, and mosaic.

Anthracnose of beans results principally in dark, sunken spots on the pods, which make such beans unmarketable. In the case of dry shell beans the seed may be discolored. Anthracnose can be eliminated from any stock of seed beans by growing the stock in any of the seed-bean-producing areas west of the Mississippi River, since conditions in such areas are unfavorable for anthracnose development.

Bacterial blights cause water-soaked spots that later throw off a gray or yellow exudate depending on the blight involved. Bacterial blights can be eliminated by growing in dry-land seed-bean areas, or in certain irrigated districts in Idaho and California.

Mosaic causes a green pattern in the leaf, and in severe cases the leaves may be distorted and the pods reduced in size. Mosaic spreads rapidly from one plant to another, and the symptoms often are not apparent. There is no place known where it is possible to eliminate mosaic from bean seeds by growing in a special environment.

In some cases organisms in the soil (frequently *Fusarium martii phaseoli* Burk.) cause severe injuries to the roots, which may reduce the stand or result in premature ripening, but such diseases are not seed-borne.

The relationship of seed-borne diseases to breeding work with various types of beans can perhaps best be explained by examples. Previous to the moving of the seed-bean industry to the West, anthracnose was the most serious bean disease. At the present time anthracnose is seldom seen in market-garden or canning varieties of beans unless the seed has been saved from an eastern-grown crop. On the other hand, anthracnose is quite common in field beans grown in the East, since most of the seed must necessarily be home-grown. New York grows large acreages of both snap and dry-shell beans, of which the latter are troubled yearly by anthracnose and the former only to a minor extent. New York State has had a vigorous breeding program in effect and has originated several strains resistant to various strains of *Colletotrichum lindemuthianum* (Sacc. and Magn.) Briosi and Cav., the organism that causes anthracnose. There has been no major program by any division of the Federal or State institutions to breed snap bean varieties resistant to anthracnose. Resistance to root-rotting organisms has been studied, but not much has been done to breed for resistance against them.

The Newer Bean Varieties

Productions by Private Breeders

In some cases improved strains not possessing any disease resistance have been introduced. Burpee Stringless Green Pod has been largely replaced by Landreth Stringless (about 1927), but the older name has been retained. The latter undoubtedly was of higher quality, but in some sections home gardeners object that the seed of the new strain does not develop quickly enough. On the other hand, quick seed development is a characteristic that shippers and most city consumers object to.

Giant Stringless, Full Measure, and Burpee Stringless have been losing popularity in competition with New Stringless Green Pod (Tendergreen). This new variety is more resistant to bacterial blights than the other three varieties and yields quite well under a diversity of conditions. It is said to come from an accidental cross of Stringless Green Refugee with Full Measure. It was introduced by Henderson in 1922 as Tendergreen, but was pure-lined, renamed, and introduced by the Associated Seed Growers, Inc., in 1930.

Asgrow Black Valentine Stringless was an introduction by the Associated Seed Growers, Inc., in 1930. It is said to come from a cross of Black Valentine with Pencil Pod Black Wax. It is interesting to note in this connection, however, that some observers have found white and variegated seeds segregating from this variety. This bean is hardy and of very good quality—in contrast to the poor quality of Black Valentine—and is replacing the old Black Valentine rapidly in many shipping sections.

Stringless Green Refugee is very resistant to bacterial blights but extremely susceptible to common bean mosaic and to many other viruses infecting beans, as described by Zaumeyer and Wade (*95*) and Pierce (*51*). In some sections severe economic losses from common bean mosaic on this variety have occurred.

In spite of the specialized machinery developed for canning beans, snap bean varieties have remained essentially general-purpose varieties. However, in a few cases canning has tended to intensify the importance of certain varieties. Stringless Green Refugee has set a standard that canners have sought in an early variety. Stringless Green Refugee is a late, light-green-podded bean, stringless, essentially free from fiber in the side walls, fine-textured, and with small, straight, nearly round pods. It has been used mainly for packing whole, but any oversized pods are excellent for packing as cut beans. Some canners are not interested in the whole pack and can use a variety that will produce a large yield of beans of only moderate quality. In some sections Full Measure is the favorite. It is early, dark-green podded, stringless, essentially free from fiber in the side walls, medium to coarse in texture, with large pods. Where essentially the same qualities are desired but with lighter pods, Giant Stringless Green Pod is used. Flat beans are seldom canned. In the wax types a white-seeded early wax with the quality of Refugee Green is desired. The nearest approach is Brittle Wax, but canners object to the large eye, which can sometimes be seen in the processed beans.

Bean Breeding by Public Agencies

The United States Department of Agriculture began breeding work in 1922 to produce a Refugee type of bean resistant or tolerant [5] to mosaic. This work was started by Wilbur Brotherton in cooperation with the Wisconsin Agricultural Experiment Station and was later carried on by G. H. Rieman, W. J. Zaumeyer, and the writer. The first introduction was U. S. No. 1 (1933), an early mosaic-tolerant strain intermediate in type between Refugee and Full Measure. It has been favorably received in limited areas only and will probably remain of minor importance. The second Refugee type introduced by the Department came in 1935 and is designated U. S. No. 5. All reports on this bean have been very favorable. It is highly resistant to common bean mosaic and tolerant to bacterial blight, and the pods are not distinguishable from Refugee except that those of U. S. No. 5 are free from purple splashing caused by anthocyanin pigment. U. S. No. 1 is from the tenth generation of a cross of Refugee × Wells Red Kidney, and U. S. No. 5 is from a cross of U. S. No. 1 with a mosaic-resistant Refugee rogue. Previous to the introduction of U. S. No. 1 and U. S. No. 5, Rieman, in cooperation with the Wisconsin station,

[5] In this discussion the word "tolerant" is used to describe a variety that suffers no appreciable reduction in yield as a result of infection, although other disease symptoms may be clearly shown. "Resistant" refers to varieties that are apparently unaffected by the disease in any way.

had made fairly extensive tests of No. 536 Canning Wax, which did not prove to be commercially successful but which has since been used in breeding work for mosaic resistance and for quality of pods.

The Wisconsin station began breeding work with Refugee × Corbett Refugee (a rogue type), from which came Wisconsin Refugee and Idaho Refugee, both introduced in 1934. Wisconsin Refugee is about the same in season as Stringless Green Refugee. It is mosaic-resistant, but the type is not so well fixed as Idaho Refugee. Idaho Refugee is about a week earlier than Stringless Green Refugee. It is resistant to common bean mosaic and is being favorably received by the canning trade. The pods carry a slightly heavier purple splashing in both Wisconsin Refugee and Idaho Refugee than in the parent varieties, although there is a possibility of eliminating this by further selection. W. H. Pierce and J. C. Walker introduced these two strains.

The first bean to be bred especially for mosaic resistance was Robust. It is a strain of Michigan Pea bean (dry shell) and was introduced by F. A. Spragg, of the Michigan Agricultural Experiment Station, about 1913 from field selections.

W. H. Pierce and C. W. Hungerford, of the Idaho station, introduced Idaho No. 1 Mosaic Resistant Great Northern about 1930. It is a very hardy dry-shell bean obtained by selection from heterogeneous strains of Great Northern.

Further work on resistance to mosaic in snap beans is being carried on at the Michigan station by C. H. Mahoney and at the New York stations at Geneva and Ithaca.

One of the most interesting developments in connection with canning string beans is the sudden popularity of a strain of White Creaseback known in some places as Blue Lake. This is somewhat different from the ordinary strains of White Creaseback grown in home gardens. The pods are very long, dark-green in color, and round in cross section at a very early stage. Nearly all beans canned from this variety are put up in whole lengths in "asparagus" style. The popularity of this excellent dark bean may mean the beginning of a new era in American bean breeding, since the proponents of light-podded Refugee types can no longer consistently claim that high quality in a canning bean is associated only with light-green pods.

Bean rust is another problem that has required attention during the last few years. Kentucky Wonder and most strains of white-seeded Kentucky Wonder are susceptible to strains of rust. In 1934 L. L. Harter, of the Bureau of Plant Industry, United States Department of Agriculture, introduced U. S. No. 3 and U. S. No. 4 strains of white-seeded, rust-resistant Kentucky Wonder. These were pure-line selections from heterogeneous strains from Europe known as World Wonder and Phenomenon, respectively. U. S. No. 3 has been very favorably received. It is a very early pole bean, coming in bloom only a few days later than Full Measure. The pods are large, round, stringless at all stages, and of high quality. U. S. No. 4 is somewhat later than U. S. No. 3, and the pods are very long, flat, and stringless in early market stages. They represent an improved strain of what would ordinarily be considered white-seeded Kentucky Wonder. Further breeding work is under way involving crosses of

138904°—37——18

brown-seeded Kentucky Wonder with U. S. No. 3 and U. S. No. 4 and for resistance to other strains of rusts.

In connection with the bean-breeding program of the Department several green and wax canning, market-garden, and pole strains resistant to various diseases are now in the course of development. These are being bred and tested for the most part at Greeley, Colo., Charleston, S. C., and Beltsville, Md. Those now engaged in this work are W. J. Zaumeyer, L. L. Harter, and W. D. Moore in pathology, and the writer and C. F. Poole in genetics. For the last few years S. A. Wingard, of the Virginia Agricultural Experiment Station, has been developing strains of the Kentucky Wonder type suitable for growing in that State and resistant to rust. He has succeeded in establishing very satisfactory late strains that are not early enough for growing seasons in northern or north-central regions.

List of Varietal Introductions

Table 1 shows in a condensed form some of the outstanding bean varietal introductions of the last 20 years or so.

Table 1.—*Bean varietal introductions*

Variety or strain	Type	Special characteristics	Introduced by—
Robust	Dry shell (pea bean)	Resistant to common bean mosaic.	F. A. Spragg, Michigan, 1913.
Idaho No. 1 Great Northern	Dry shell	do	Pierce and Hungerford, Idaho, 1930.
Geneva Red Kidney	do	Resistant to strains of anthracnose.	Gloyer, 1928.
York Red Kidney	do	do	Do.
Virginia Kentucky Wonder	Snap pole	Resistant to rust	Wingard, 1934.
U. S. No. 3	do	do	Harter, 1934.
U. S. No. 4	do	do	Do.
U. S. No. 1	Refugee	Tolerant to mosaic	Wade and Zaumeyer, U. S. Department of Agriculture, 1933.
U. S. No. 5	do	Resistant to mosaic	Wade and Zaumeyer, U. S. Department of Agriculture, 1935.
Idaho Refugee	do	do	Pierce and Walker, University of Idaho, 1934.
Wisconsin Refugee	do	do	Walker and Pierce, University of Wisconsin, 1934.
Corbett Refugee	Refugee rogue	do	Corbett, Sioux City, Iowa, 1931.
No. 536	Canning wax	Resistant to mosaic, small pods.	Rieman, 1928, U. S. Department of Agriculture and University of Wisconsin.
Blue Lake	White Creaseback	High-quality, dark-podded canner for whole-length packs.	Clear Lake Canneries (?), about 1930.
Asgrow Black Valentine	Stringless Valentine	Stringless	Associated Seed Growers, 1930.
Tendergreen	Full Measure	Tolerant to bacterial blights.	Henderson, 1922.
New Stringless Green Pod	do	do	Associated Seed Growers, 1930.
Landreth Stringless Green Pod.	Burpee Stringless	Refined pod	Landreth, about 1927.
Stringless Red Valentine	Red Valentine	Stringless	Landreth, 1930.

The development of new disease-resistant varieties of beans has done much to stimulate pure-line work among the seed companies, and many have greatly improved the standards of their basic seed stocks and of the stocks they deliver to canners and to market and home gardeners. The complex nature of present-day breeding work makes it necessary for seed companies to employ plant breeders with an adequate knowledge of genetics and plant pathology.

LIMA BEANS

ALTHOUGH the botanical differences between lima beans (*Phaseolus lunatus* L.[6]) and common beans (*P. vulgaris*) are not great, it has so far not been possible to cross the two species. The most conspicuous difference is in the flower bracts. They are small, inconspicuous, lanceolate, and pointed in *P. lunatus* and large, conspicuous, and oval in *P. vulgaris*.

Lima beans cannot be grown as far north as common beans. In the South or in the Tropics if a set of blossoms is dropped because of drought or very hot weather, the long growing season still may give plenty of time for beans to be set later. Where the seasons are shorter, failure of the crop may result from the loss of the first blossoms. In California the long growing season makes it unnecessary for the first blossoms to develop into pods.

Limas became popular in the United States after 1824, when seed of the large type—as contrasted with the small-seeded civet or sieva type—was brought from Lima, Peru, by Capt. John Harris, of the United States Navy. It was found that the lima did especially well on the dry lands of southern California. The two limas now most extensively grown are both dwarf varieties, Henderson Bush and Fordhook. Henderson Bush was found along a roadside in Virginia by a Negro laborer about 1885. He sold it to T. W. Wood & Sons, of Richmond, who later sold the stock to Peter Henderson. It is a small erect bush type with very small, flat seeds. It can usually be counted on to produce a crop even under adverse conditions. Wood Prolific Bush, a later selection from Henderson Bush, is a slightly larger plant. U. S. No. 2 lima (1933) is a selection from Henderson Bush developed especially for uniform maturity of the pods on the individual vine. It is not distinct enough to constitute a variety, but under some conditions it may be from a few days to 2 weeks earlier than most strains of Henderson Bush. Henderson Bush and related types are grown to some extent in home gardens but are more generally used for commercial canning.

Canners have wished to combine the hardiness and yield of Henderson with the quality of Fordhook. In 1934 the McCrea Seed Co. introduced the McCrea lima, which is green-seeded when mature, of high quality, but late and not an especially good yielder in eastern canning districts. The green seed character is not apparent in either Henderson or Fordhook, so it is probable that the parentage is some large, green-seeded variety crossed with Henderson.

Fordhook, a large-seeded dwarf plant, was discovered in a field of Challenger pole limas by Henry Fish, of Santa Barbara, Calif., in 1903. Burpee introduced it in 1907. It is now the favorite market-garden variety. A small quantity is canned, but its popularity for canning has not been great because of its sensitiveness to adverse weather conditions.

[6]In ordinary botanical usage *Phaseolus lunatus* is the civet or sieva bean and *P. lunatus macrocarpus* Benth. the lima bean.

During the last several years the California Agricultural Experiment Station has introduced strains of a very hardy, high-yielding, small-seeded lima known as Hopi, selected by Mackie from limas grown by the Hopi Indians. Most of the Hopi and Henderson Bush grown in California are used as dry, edible beans.

A very noteworthy fact about lima bean breeding is that practically all varieties have arisen by selection and very few from controlled breeding work. Roy Magruder, of the Bureau of Plant Industry, is at the present time carrying on considerable breeding and genetic work involving seed-coat colors, seed sizes, and the breeding of various types for canning.

In the southern United States pole limas with either colored or white seeds are grown extensively in home gardens and to some extent for marketing under the name of butter beans. These are very hardy varieties and probably offer worth-while breeding material for crossing with nonhardy, high-quality varieties such as Fordhook.

GENETICS OF PEAS AND BEANS [7]

PEAS

THE many stable forms of *Pisum sativum* early attracted the attention of those interested in theoretical scientific work as well as the attention of many breeders. It was with garden peas that Gregor Mendel in 1856 began his historic experiment, which laid the foundation for genetic science. His findings were made public in 1865 but attracted no attention until they were rediscovered by Correns, De Vries, and Tschermak independently in 1900.

Mendel worked with seven different factors: Yellow *v.* green cotyledons, smooth *v.* wrinkled seed coats, normal *v.* fasciated stems, tall *v.* dwarf growth habit, green *v.* yellow pods, parchmented *v.* nonparchmented pods, and the pleitropic factor for colored *v.* colorless seed coats, colored *v.* colorless leaf axils, and purple *v.* white flowers. A pleitropic factor is one that affects many different characters.

In spite of Mendel's success with the plant, peas have not proved to be ideal for genetic studies, and consequently most of the fundamental contributions since his time have been with organisms other than peas. There are probably several reasons for this: (1) Many single-factor differences frequently show wide divergences from a 3:1 ratio. (2) Linkage values may vary sharply from one cross to another. (3) Different classification of phenotypes gives rise to reports of more than 50 percent crossing over. (4) The number of independent factors and groups of factors appears to exceed the number of chromosomes. (5) Peas have proved to be rather difficult material for cytological studies.

Wellensiek (*85*) brought the available data up to date and has worked unceasingly to eliminate conflicts in designations of various factors. Matsuura (*39*) also reviewed and tabulated the literature dealing with *Pisum* genetics. The following lists of factors are taken largely from Wellensiek, with a few modifications by De Haan (*11*) and Winge (*92*). The number of genes listed is 68, but the known number may be in excess of this. In some cases it has been difficult

[7] This section is written primarily for students or others professionally interested in breeding or genetics.

to decide whether some ratios are the result of pleitropic effects of a single gene or the effect of several genes completely linked. Winge gives a table showing certain gene designations made by himself and 10 other authors, including De Winton (*93*), Wellensiek (*86*, *87*, *88*, *89*, *90*), Rasmusson (*55*, *57*, *58*), White (*91*), Lamprecht (*30*), Pellew and Sverdrup (*49*), Sverdrup (*70*), Nilsson (*42*), Kajanus (*21*, *22*), H. and O. Tedin (*72*, *73*), and De Haan (*11*).

Pisum Factors

A. Basic gene for anthocyanin color of the flower. It also influences indenting of seeds, seed-coat color, marbling of seed coat (except ghost marbling), leaf-axil color, violet and red pod colors.
A_1, crypto purple; A_2, purple dotted flowers; *a*, white.
Ar. Gene for reddening, salmon-pink flowers.
Ap. Apple blossom.
Am. Pinkish-white flowers.
B. Gene for bluing.
Bl, basic gene for wax or bloom; *bl*, waxless (emerald).
Bta, blunt apex; *bta*, acute apex. } Both recessives must be present in homozygous
Btb, blunt apex; *btb*, acute apex. } condition to produce acute.
Cp, curved pod; *cp*, straight.
Cr. Changes crimson to purple in presence of *A*. (Fedotov (*7*).)
Cv. Intensifies anthocyanin color in presence of *A* and *B*. (Fedotov (*7*).)
Cm. Cream flowers. (Fedotov (*7*).)
Em^1, Em^2, normal; em^1, em^2, emergences if both are present.
Ep'_1, Ep_1 } Thickness of seed coat. (Kaznowski (*23*).)
Dw, *D*, *d*. Leaf axil ring double, single, absent. (Tedin and Tedin (*72*).)
F. Purple dotting of seed coat I. (Wellensiek.)
F_s. Purple dotting of seed coat II. (Winge.)
Fe, normal pods, fertile; *fe*, split pods, sterile as female. (Sverdrup (*70*).)
Fa, normal stem; *fa*, fasciated stem.
Fu, resistant to fusarium wilt; *fu*, susceptible.
Fl, gray spotting on leaves; *fl*, green leaves.
Fn, one or two flowers per peduncle; *fn*, three or more flowers per peduncle.
G, green cotyledon; *g*, yellow cotyledon. (Nilsson (*42*).)
Gp, green pod; *gp*, canary yellow pod.
H. With *A* gives orange seed coat.
I. Inhibits action of *G*, giving dominant yellow cotyledons.
If, intermediate flowering; *if*, early flowering.
J. In presence of *A*, causes dark-brown seed coat.
K, normal wings; *k*, keeled wings.
Kl. Inhibits coupling between *A* and *Gp*. (Hammarlund (*13*).)
L, L_1, L_2. Genes for wrinkling or dimpling of seed.
Le, Le_1, *le*. Long, very long, and short internodes.
La. Growth-inhibiting factor. (De Haan (*11*).)
Lb. Growth-inhibiting factor.
Lc. Growth-inhibiting factor.
Ld. Growth-inhibiting factor.

(*Le* dominates if *La* or *Lb* is present, but not if the two recessives, *la*, *lb*, are present. Either *Le*, *la*, *lb*, or *le*, *la*, *lb* is slender. 45:15:4 segregation of tall, short, slender in F_2.)

Lf. Retards flowering time caused by *If*; ineffective by itself.
Lo, Lo_1, Lo_2, Lo_3. Genes for seed length. (Kaznowski (*23*).)
M with *Z* gives "ghost marbling" of testa; with both *A* and *Z*, brown marbling.
M_1 to M_4. Genes for susceptibility to mildew. (Hammarlund (*13*).)
Mp. Rusty radicula. (Tedin and Tedin (*73*).)
N, thin pod wall; *n*, thick pod wall.
Nr, normal; *nr*, narrow rogues. (Pellew (*48*).)
O, *or*, *oy*. Green, lemon, gold pods, stems, and foliage.
Oh. Inhibits the expression of red, converts red to bright-brown seed coat.
P. Thin parchmented membrane in pod; *p*, no membrane.

P_1. Purple pod I } Both dominants necessary to make pod purple.
P_2. Purple pod II }
Pa, green pods; *pa*, pale pods.
Pe, normal pods; *pe*, pearl pods.
Pl, dark hilum; *pl*, light hilum.
Pt. Quick growth of pollen tube.
Q, aborted seed; *q*, normal seed. (Wellensiek and Keyser (*90*).)
R, round seed; *r*, wrinkled seed surface.

(*R* is hypostatic to *A*; *r* is epistatic to *A*. In conjunction with genes L_1 and L_2 of Hadfield and Calder (*12*), the following forms may be distinguished: Smooth, $l_1\, l_1\, l_2\, l_2\, RR$; dimpled, $L_1\, L_1\, L_2\, L_2\, RR$; wrinkled, $L_1\, L_1\, L_2\, L_2\, rr$; wrinkled, $l_1\, l_1\, L_2\, L_2\, rr$).

Re, normal leaves; *re*, reduced leaves.
S, seeds free in pod; *s*, seeds clinging together (chenille or brochette).
Sa_1, Sa_2, Sa_3. Genes for number of stomata. (Tavčar (*71*).)
Sg_1 to Sg_4. Genes for seed weight.
Sn_1, intermediate value for node number; sn_1, low value.
Sn_2, increases the value for node number caused by Sn_1; ineffective alone.
St, normal stipules; *st*, reduced stipules.
T, T_1, T_2. Genes for internode number.
Td, leaves dentate; *td*, leaves not dentate.
Tl, tentril leaves; *tl*, acacia (no tendrils).
U, violet seed coat.
Uni, Normal leaf; *uni*, unifoliate.
V, Strong membrane in pod; *v*, thin membrane.
Wb_1. Strengthening gene for wax.
Wb_2. Strengthening gene for wax.
W_2, green foliage; w_2, white variegated.
X. Stipule size. (Brotherton (*1*).)
Y. Stipule size.
Z, colored seed coat; *z*, uncolored seed coat.

As there are many factors influencing flower color, it is perhaps best to illustrate the genetic constitution of some of the many colors that occur. These are given from De Haan (*11*):

Purple	*A A Ar Ar B B Ap Ap Am Am*
Violet	*A A ar ar B B Ap Ap Am Am*
Rose	*A A Ar Ar b b Ap Ap Am Am*
Light purple	*A A ar ar b b Ap Ap Am Am*
Apple blossom	*A A Ar Ar B B ap ap Am Am*
Apple rose	*A A Ar Ar b b ap ap Am Am*
Apple violet	*A A ar ar B B ap ap Am Am*
Pinkish white	*A A Ar Ar B B Ap Ap am am*
White	*a a Ar Ar B B Ap Ap Am Am*

A cross of violet by apple rose results in a purple F_1 with a trihybrid ratio in F_2 of 27 purple : 9 violet : 9 apple blossom : 9 rose : 3 apple violet : 3 apple rose : 3 light purple : 1 expected to have an appearance between apple rose and light purple. According to the above scheme, all those having *aa* are white regardless of the rest of the genetic constitution. A certain white[8] × apple blossom results in an F_2 segregation of 9 purple : 3 apple blossom : 4 white. According to the designations of Fedotov (*7*), *Cm* can produce a cream flower and it is independent of the action of *A*.

In addition to flower color, the genes that have been listed have an influence on color of the leaf axil. Purple and apple-rose flowers are associated with purple axils; pinkish white, with dull-rose axils; violet and apple violet, with violet; rose and apple rose, with rose; and light purple, with light purple. *Dw* produces a two-ring effect in the axils, *D* a single ring, and *d* no ring.

[8] Only the white of the constitution *aaArArBBApApAmAm* will give the ratio cited when crossed with apple rose.

There is considerable variation in the amount of waxiness or bloom on peas. Waxiness is caused by a gene for wax *Bl*, and is intensified by the presence of either $W^b{}_1$ or $W^b{}_2$ or both.

Two genes (bt_a and bt_b) must be present in the homozygous condition for a pod to have an acute apex. Crosses between strains with blunt pods and those with sharp result in the F_2 either in a ratio of 15 blunt : 1 acute or of 3 : 1, depending on how many of the genes for bluntness were present in the blunt parent. There is at least one other factor influencing pod-apex shape.

The gene *fe* is responsible for a rather peculiar condition in which the developing pods split along the dorsal suture, resulting in the death of the developing seeds.

The fasciated or flattened stem condition is due to a recessive gene, *fa*. This flattened condition results in a terminal inflorescence that superficially resembles an umbel. Some flower stalks may produce from three to seven flowers, while others produce only one or two on the same plant.

Tallness and shortness in pea plants have long been of much interest, and it has been discovered that many factors are concerned with stem length. In some cases simple 3 : 1 ratios of tall to short are obtained in the F_2 generations from crosses of tall with short. In one such cross, however, De Haan (*11*) obtained an F_2 segregation of 45 tall : 15 short : 4 slender. Two recessive genes must be present to produce a slender plant. Gene *Le* is epistatic to *La* or *Lb* but hypostatic to *la* or *lb*. Genes *lc* and *ld* result in a slightly larger short plant designated "short 2." One of the factors for slender is identical with *lc* or *ld*, but it has not yet been determined which.

The edible-podded condition (no membrane) is determined by the recessive gene *p* in the homozygous condition. The factor *V* results in a very strong membrane when acting in conjunction with *P*.

Pt is a theoretical gene for quick growth of the pollen tube. Its presence has never been determined by actual ratios.

Round seeds are dominant to wrinkled, and segregation is by individual seeds. Several genes influence the condition known as indenting or dimpling, and segregation is by plant. A three-factor explanation has recently been given (*12*) of the conditions designated smooth, dimpled, and wrinkled, respectively.

Seed weight is influenced by several factors, the exact number of which has never been determined. Violet flower is sometimes associated with abnormal hilum, which results in low seed weights on plants having violet flowers. Many other factors also probably influence seed weights.

The Gradus rogue (rabbit ear) character (*1*) is a rather unique condition in which very rapid mutation of the recessive gene *x* for normal Gradus type to the dominant *X* (rogue) occurs when these genes are associated together in a cross. While other factors involved in a cross may be segregating as expected, no plants of normal type may be recovered in F_2 or subsequent generations.

Seed-coat colors are also affected by the gene *A* for anthocyanin. Factors *Ar* and *B* have an effect on seed-coat color parallel with their effects on flower color, but *Am* and *Ap* have no effect on seed coat. The effects of *Pl*, *M*, *F*, *Oh*, *Z*, and *Mp* on flower color are known.

Disease Resistance

Hammarlund (*13*) reported that immunity of peas to powdery mildew was due to the presence of four genes, M_1, M_2, M_3, and M_4. The varieties commonly grown in the United States are all susceptible to powdery mildew, but artificial control methods have been effective in preventing damage by this organism. Neither genetic nor breeding investigations of powdery mildew resistance have been undertaken in this country.

Wade (*82*) reported that resistance to fusarium wilt of peas was due to a single dominant gene, *Fu*. This was slightly linked with *Le*. Extensive breeding work has been carried out by many workers, and

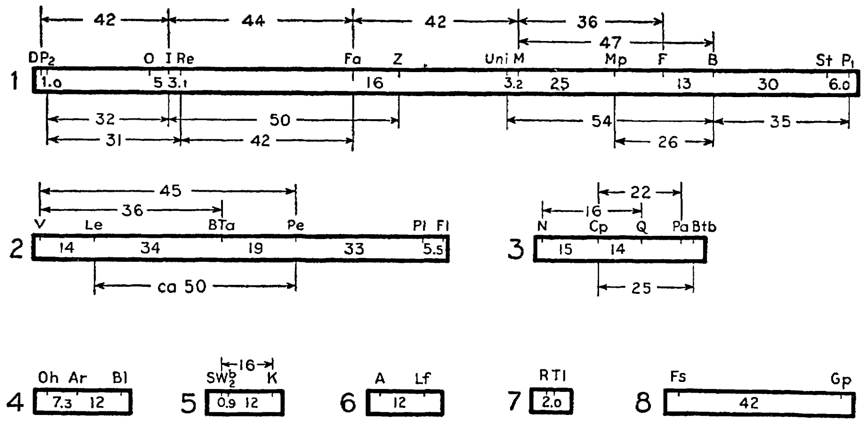

Figure 1.—Linkage groups in *Pisum*. (After Winge.)

at the present time all the canning varieties are available in wilt-resistant forms.

Zaumeyer and Wade (*96*) have shown that different varieties of peas show differential reactions to various types of legume mosaics. The presence of many diseases, frequently epidemic in nature, indicates that in the future much work will be done in connection with the inheritance and breeding of disease-resistant strains of peas.

Various reports have shown that many varieties of peas possess some tolerance to the attacks of various root-rotting organisms, but the genetic bases of these reactions have not been determined.

Linkage and Cytology

The contribution of Winge (*92*) on linkage in *Pisum* has greatly clarified the linkage situation. He describes eight linkage groups, which are here redrawn (fig. 1) from his publication.

It is believed that further research will eventually reduce the number of linkage groups to seven, to correspond with the number of pairs of chromosomes known to be present in *Pisum sativum*.

Ring formation (*9*) seems to be the most satisfactory explanation of many of the variable linkage results obtained by Rasmusson, Wellensiek, Tedin and Tedin, and other workers. Although Rasmusson (*56*) shows the genetic nature of some linkage intensities, the number of factors involved in the segregation of these intensities is not known. Håkansson (*10*) reports a semisterile condition in association with chromosomal exchange. Sutton (*69*) reports an instance of half disjunction in a case involving four chromosomes.

Beans

The literature on bean (*Phaseolus vulgaris*) genetics and breeding is very extensive. Kooiman (*24*) presents a very thorough review of the subject and does much to clarify conflicts in terminology. Doornkaat-Koolman (*4*) had previously reviewed the literature, especially that dealing with disease resistance. Matsuura (*39*) also presents a summary. Much of the material in this paper is drawn from reviews by these authors, with stress on literature published since 1929.

Inheritance in beans has been investigated for a long time, but there are still many divergent results that need further studies for adequate interpretation. This is especially true with regard to flower colors and their relationship to seed and pod colors.

Shaw (*66*) and Shaw and Norton (*67*) present extensive observations on flower colors, which indicate that at least two factors must interact for the production of pigment in flowers. According to their observations, most varieties with pigmented seeds, with the exception of Red Valentine, have colored flowers. However, many other exceptions to the observations of these authors are now known.

Johannsen (*19*) obtained a dihybrid ratio in progeny from a cross of a white-flowered brown-seeded bean variety with a violet-flowered black-seeded one.

Tjebbes and Kooiman (*76*) explain the results of a spontaneous cross of violet × lilac-flowered, in which dark violet, light violet, lilac, and white flowers appeared in association with red and blue pods and various seed colors on the basis of three genes. *R* causes red pod striping whether or not the ground factor *A* for seed-coat color is present. When *A* is present the flowers are lilac; the seed coat is red, due to *R*. *Bl* changes these colors to bluish tints. Heterozygous *Bl bl* results in light violet. They assumed a total of seven genes for flower color.

Kooiman (*24*) suggested an eight-factor explanation of the various seed-coat colors encountered.

Sirks (*68*) presented a factorial explanation of various seed-coat colors and summarized the literature up to that date.

Lamprecht (*25, 26, 27, 28, 29, 31, 32, 33, 34, 35*) has presented a very satisfactory explanation of most of the seed-coat colors encountered in beans. He assumes eight pairs of genes and the following interactions among them:

P. Basic color factor, in itself producing no color.
C with *P* gives sulphur white; *Cc*, mottled.
J. Pale ecru in seed coat, also in hilum.
G with *PCJB* gives mineral brown; with *PCJV* gives maroon brown; with *PCJBV* gives black; with *Ca* gives caruncle streak.
B with *PCJG* gives mineral brown; when heterozygous with *PCJVv* gives dark dull green; when homozygous with *PCJV* or *PCJVG* gives black.
V with *PCJG* gives maroon brown; when heterozygous with *PCJBb* gives dark dull green; when homozygous with *PCJB* or *PCJBG* gives black.

R. Red.
Ca. Caruncle streak; shows only in presence of G.
PCJ. Chamois color.
PCJG. Blister (yellowish brown).
PCJgB. Golden bronze yellow.
PCJgbV. Violet purple.
PCJGB. Mineral brown.
PCJGV. Maroon brown.

(Chamois, *PCJ*, in the presence *G* and *B* gives mineral brown; *G* and *V* give maroon brown; *B* and *V*, both heterozygous, produce dark dull green; while *B* and *V*, either homozygous or in the presence of *G*, produce black.)

PCJBbVv. Dark, dull green.
PCJBVG. Black.

Micropyle streak is recessive and will not show in the presence of either or both inhibiting factors *Mi* and *Mia;* furthermore, *J* is necessary for its expression even when the inhibitors are absent.

Later, Lamprecht (*33*) has shown that factors *J* and *R* are inherited independently, and that in addition to the *Cc* inconstant marbling there is also *Rr* inconstant marbling.

Schreiber (*64, 65*) explains his results on a somewhat different basis. Genes M_1 and M_2 must both be present to produce a constant marbling effect. *B* is a factor for light brown; *C* is an intensifier. *D* is for dark green, effective only in the presence of the basic color factor *A* or *P*. *L* inhibits partial spotting caused by Shaw and Norton's "*T*". Miyake, Imai, and Tabuchi (*41*) found all seed-coat colors hypostatic to black.

Tschermak (*78*) suggested two genes for eye pattern:

(1) $z_1z_1Z_2Z_2$. Seeds having half or more of the testa pigmented with sharp limits.
(2) $z_1z_1Z_1z_2$. Seeds having half or less pigmented, without sharp limits.
(3) $z_1z_1z_2z_2$. Pigment confined to a small hilum spot.

Sax (*60*) found in his crosses of two types of Yellow Eye beans that the heterozygous condition resulted in a pigmented area exceeding twice that of the parents. Only a single gene was involved.

Currence (*3*) found two distinct types of bean pod stringiness, one due to two dominant complementary genes, the other to an incompletely dominant gene for stringlessness with an inhibiting factor. Joosten (*20*) distinguished 10 classes of stringiness. Prakken (*53*) found 15 stringless to 1 stringy in an F_2 generation.

Tschermak (*78*) observed 3:1 and 13:3 ratios in F_2 for nonconstricted versus constricted pod. Lamprecht (*26*) interpreted his results on the basis of four factors.

Emerson (*5*), Lock (*36*), Doornkaat-Koolman (*4*), and Tschermak (*79*) found green pods dominant over yellow (wax) with a 3:1 ratio in F_2. Currence (*3*) found two factors to determine the difference between these characters.

Tschermak (*79*) found a single factor difference between round versus flat, with round dominant. Wóycicki (*94*) and Currence (*3*) found several factors involved.

Miyake, Imai, and Tabuchi (*41*) have studied the inheritance of color of stem. Two types of green crossed together gave a red F_1, followed by a segregation of 9 red : 7 green in F_2. Pink × green gave 9 red : 3 pink : 4 green.

Emerson (*5, 6*) shows that there are three factors involved in bean height: (1) Determinate versus indeterminate growth; (2) number of internodes (in pole beans this depends largely on environmental conditions); (3) internode length.

Norton (*45*) interprets his results by means of three factors governing height:

A–a. Indeterminate *v.* determinate.
L–l. Tall *v.* short.
T–t. Twining *v.* nontwining.
ALT. Pole beans.
ALt. Runner beans, nontwining pole.
Alt. Shoots from main axis short; some few early, twining shoots.
aLT and *aLt.* Spreading forms with long branches.
alT and *alt.* Erect, bush.

Three-to-one segregations of tall to short have been observed by McRostie (*37*), Tjebbes and Kooiman (*76*), and Doornkaat-Koolman (*4*).

Table 2 gives some bean characters not considered above.

TABLE 2.—*Bean characters*

Contrasted characters	F_2 segregation	Author
Blunt *v.* sharp leaf apex	3:1	Tschermak (*78*).
Broad *v.* narrow leaf	Complex	Emerson (*5*), Wóycicki (*94*).
Long *v.* short internode	do	Tschermak (*78*), Wóycicki (*94*).
Nonparchmented *v.* parchmented pod	3:1	Emerson (*5*), Tschermak (*78*), Wellensiek (*84*).
Threshable *v.* difficult to thresh	3:1	Tjebbes and Kooiman (*76*).
Yellow *v.* green cotyledon	3:1	Tschermak (*78*).
Yellow *v.* chamois seed	3:1	Nilsson (*43*).
Straight *v.* curved pods	3:1 and 2 modifying factors.	Lamprecht (*26*).
Round *v.* elliptical pods	3:1 and bifactorial	Do.
Normal *v.* unifoliate leaves	3:1	Lamprecht (*35*).
Partially colored seeds	4 or 5 genes	Lamprecht (*31*).
Unlimited *v.* limited growth of axil	3:1	Lamprecht (*34*).
Unbranched *v.* branched inflorescence	3:1	Do.

Disease Resistance

Several strains are known of the organism *Colletotrichum lindemuthianum*, causing bean anthracnose. Burkholder (*2*) and McRostie (*37, 38*) have studied the inheritance of resistance. Where one strain of fungus was concerned, a ratio of 3 resistant to 1 susceptible was obtained; two strains resulted in a 9:7 ratio. Further work is being done on this problem at Cornell University and in the United States Department of Agriculture.

Schreiber (*64*) indicates that there are three independent factors for resistance corresponding to three anthracnose strains.

McRostie (*38*) in crosses involving Robust Pea bean × Flat Marrow observed the F_1 showing a partial dominance of susceptibility. F_2 indicated at least a two-factor difference. Pierce (*52*) and Parker (*47*) have studied the inheritance of resistance to common bean mosaic, using different bean varieties. Parker concluded that since reciprocal crosses gave different results, at least part of the material for resistance was carried in the plant outside the chromosomes. Pierce did not attempt to show a genetic interpretation.

It is interesting to note in connection with the maternal inheritance suggested above that Hoffman (*16*) found that modifications persisted for six generations after he had treated navy beans with chloral hydrate. These modifications were transmitted only by the cytoplasm of the egg cells and not through the chromatin. It is also of interest to note that Parker (*46*) has found an undoubted case of maternal inheritance of leaf variegation.

Zaumeyer and Wade (*95*) and Pierce (*51*) have indicated that more than one strain of bean mosaic or of legume viruses transmissable to beans are in existence and that bean varieties differ in their reactions to them. Genetic studies of varieties resistant to the viruses are now in progress in the Department.

Rands and Brotherton (*54*) tested the resistance of many varieties and strains of American and foreign beans to several diseases, including at least three strains of the anthracnose organism, bacterial blight, bacterial wilt, and mosaic, and found differential reactions in some cases.

Fromme and Wingard (*8*) made a report on resistance and susceptibility of various bean varieties to rust. There is much material available for genetic and breeding studies in connection with this disease.

McRostie (*38*) made some observations on the inheritance of resistance to dry root rot of beans, caused by *Fusarium martii phaseoli*, but he did not attempt to give a factorial explanation of his results.

Crossing Technique and Interspecific Hybridization

Beans are somewhat difficult to cross, since the curled and brittle style of the flower is easily broken during the process of opening the keel. If the atmosphere is kept near the saturation point for a few days after artificial pollination has been effected, the chances for success are much better than in only a moderately moist atmosphere. The time required to make crosses has prevented genetic studies in *Phaseolus* involving backcrosses.

Many attempts have been made to secure interspecific hybrids within *Phaseolus*, mostly without success except for that involving *P. vulgaris* and *P. multiflorus*. In such hybrids there is usually a great deal of sterility and variability in results, even in the F_1. Mendel (*40*), Doornkaat-Koolman (*4*), Tschermak (*78*), and Tjebbes (*74*) have made studies involving this interspecific cross. At the present time the United States Regional Vegetable Breeding Laboratory, near Charleston, S. C., is testing a variety from Mexico that arose from the cross of *P. vulgaris* with *P. multiflorus*.

Linkage and Cytology

Weinstein (*83*) has shown that *Phaseolus vulgaris* and all other species of *Phaseolus* have 11 pairs of chromosomes.

Tjebbes (*75*) recognizes two linkage groups. Linkage in the *B–A–R–S* group is very close, showing a cross-over value of less than 1 percent between *B* and *S*. *S* is a factor for striping and the other three factors influence the seed-coat color. Genes *C* and *G* are in another group with a cross-over value of about 35 percent.

Several factors give pleitropic effects or the effects are in reality due to more than one factor. However, in such cases it usually requires extensive work to establish the nature of the gene or the closeness of the linkage involved.

Sax (*60, 61, 62, 63*) attempted to analyze quantitative characters by studying their linkage relations to qualitative genes. He demonstrated at least five cases of linkage.

Lima Beans

Only a very limited amount of genetic work has been done with the lima bean (*Phaseolus lunatus* L.). Rhind (*59*) reports genetic studies involving three factors, which he designates as—

R. Rose color seed coat.
S. Speckled seed coat.
P. Intensifies rose to purple seed coat.

Roy Magruder, of the Bureau of Plant Industry, is carrying on genetic studies with *Phaseolus lunatus*.

LITERATURE CITED

(1) Brotherton, W., Jr.
1923. Further studies of the inheritance of "rogue" types in garden peas (Pisum sativum L.). Jour. Agr. Research 24: 815–852, illus.

(2) Burkholder, W. H.
1918. The production of an anthracnose-resistant white marrow bean. Phytopathology 8: [353]–359.

(3) Currence, T. M.
1930. Inheritance studies in Phaseolus vulgaris. Minn. Agr. Expt. Sta. Tech. Bull. 68, 28 pp., illus.

(4) Doornkaat-Koolman, H. Ten.
1927. Die Brennenfleckenkrankheit der Gartenbohne im Lichte der Vererbung. Versuche zur Immunitätszüchtung bei Phaseolus vulgaris gegenüber Colletotrichum lindemuthianum (Sacc. & Magn.) und seiner Biotypen. Forsch. Geb. Pflanzenkrank. u. Immunität Pflanzenr. 4: 112–225, illus.

(5) Emerson, R. A.
1904. Heredity in bean hybrids (Phaseolus vulgaris). Nebr. Agr. Expt. Sta. Ann. Rept. 17: 33–68.

(6) ———
1916. A genetic study of plant height in Phaseolus vulgaris. Nebr. Agr. Expt. Sta. Research Bull. 7, 73 pp., illus.

(7) Fedotov, V. S.
1930. On the hereditary factors of flower color and of some other characters in the pea. (Preliminary communication.) Vsesoiuz. S'ezd Genetike Selek., Semonov. i Plemenn. Zhivotnov. Trudy (U. S. S. R. Cong. Genetics, Plant and Anim. Breeding) 2: 523–537. [In Russian. English summary, pp. 535–537.]

(8) Fromme, F. D., and Wingard, S. A.
1921. Varietal susceptibility of beans to rust. Jour. Agr. Research 21: 385–404, illus.

(9) Håkansson, A.
1929. Chromosomenringe in Pisum und ihre mutmassliche genetische Bedeutung. Hereditas 12: 1–10, illus.

(10) ———
1934. Chromosomenbindungen in einigen Kreuzungen zwischen halbsterilen Erbsen. Hereditas 19: [341]–358, illus.

(11) Haan, H. de
1930. Contributions to the genetics of Pisum. Genetica [The Hague] 12: [321]–439, illus.

(12) Hadfield, J. W., and Calder, R. A.
1935. A genetic analysis of the seed characters wrinkled, dimpled and smooth in Pisum. Jour. Agr. Sci. [England] 25: 264–277, illus.

(13) Hammarlund, C.
1929. dritte mitteilung über einen fall von koppelung und freier kombination bei erbsen. Hereditas 12: [210]–216.
(14) Hedrick, U. P., assisted by Hall, F. H., Hawthorn, L. R., and Berger, A.
1928. peas of new york. *In* Vegetables of New York, v. 1, pt. 1, 132 pp., illus. Albany.
(15) ——— assisted by Tapley, W. T., Van Eseltine, G. P., and Enzie, W. D.
1931. the beans of new york. *In* Vegetables of New York, v. 1, pt. 2, 110 pp., illus. Albany.
(16) Hoffman, F. W.
1927. some attempts to modify the germ plasm of phaseolus vulgaris. Genetics 12: 284–294, illus.
(17) Irish, H. C.
1901. garden beans cultivated as esculents. Mo. Bot. Gard. Ann. Rept. 12: 81–165, illus.
(18) Jarvis, C. D.
1908. american varieties of beans. N. Y. (Cornell) Agr. Expt. Sta. Bull. 260, pp. 149–255, illus.
(19) Johannsen, W.
1913. mutations dans des lignées pures de haricots et discussion au sujet de la mutation en générale. 4th Conf. Internatl. Genetique, Paris, 1911, Compt. Rend. et Rapports, pp. 160–163. [In French. English summary, p. 163.]
(20) Joosten, J. H. L.
1927. een onderzoek naar het kenmaerk der "draadlossheid" bij verschillende boonenrassen. Meded. Landbouwhoogesch. [Wageningen] 31, no. 3, 49 pp., illus.
(21) Kajanus, B.
1923. genetische studien an pisum. Ztschr. Pflanzenzücht. 9: 1–22.
(22) ———
1924. zur genetik der pisum-samen. Hereditas 5: [14]–16.
(23) Kaznowski, L.
1926. studja nad grochem (pisum l.). (recherches sur le pois (pisum l.).) Pam. Państ. Inst. Nauk. Gosp. Wiejsk. Pulawach (Mém. Inst. Natl. Polon. Econ. Rurale Pulawy) 7: 1–191.
(24) Kooiman, H. N.
1931. monograph on the genetics of phaseolus, (especially ph. vulgaris and ph. multiflorus). Bibliog. Genetica 8: [296]–413, illus.
(25) Lamprecht, H.
1932. beiträge zur genetik von phaseolus vulgaris zur vererbung der testafarbe. Hereditas 16: [169]–211.
(26) ———
1932. beiträge zur genetik von phaseolus vulgaris. ii. über vererbung von hülsenfarbe und hülsenform. Hereditas 16: [295]–340, illus.
(27) ———
1932. zur genetik von phaseolus vulgaris. iii. zweiter beitrag zur vererbung der testafarbe. Hereditas 17: 1–20, illus.
(28) ———
1932. zur genetik von phaseolus vulgaris. iv. studien über genenkoppelung, mit einem fall von erblich bedingtem wechselnden crossoverprozent. Hereditas 17: [21]–53, illus.
(29) ———
1932. zur genetik von phaseolus vulgaris. v. spaltungsergebnisse nach kreuzung einer weissamigen mit gefärbtsamigen bohnenlinien. Hereditas 17: [54]–66.
(30) ———
1934. das gen uni und seine koppelung mit anderen genen bei pisum. Hereditas 18: [269]–296, illus.
(31) ———
1934. zur genetik von phaseolus vularis. vii. zwei weitere gene für sameneigenschaften, cor und fast. Hereditas 19: [163]–176, illus.

(32) LAMPRECHT, H.
1934. ZUR GENETIK VON PHASEOLUS VULGARIS. VIII. ÜBER FARBENVERTEILUNG UND VERERBUNG DER TEILFARBIGKEIT DER TESTA. Hereditas 19: [177]-222, illus.
(33) ———
1935. ZUR GENETIK VON PHASEOLUS VULGARIS. IX. ÜBER DEN EINFLUSS DES GENPAARES R-r AUF DIE TESTAFARBE. Hereditas 20: [32]-46, illus. [In German. English summary, pp. 45-46.]
(34) ———
1935. ZUR GENETIK VON PHASEOLUS VULGARIS. X. ÜBER INFLORESZENZTYPEN UND IHRE VERERBUNG. Hereditas 20: [71]-93, illus.
(35) ———
1935. ZUR GENETIK VON PHASEOLUS VULGARIS. XI. EINE MUTANTE MIT EINFACHEN BLÄTTERN UND IHRE VERERBUNGSWEISE. Hereditas 20: [238]-250, illus. [In German. English summary, p. 249.]
(36) LOCK, R. H.
1906. STUDIES IN PLANT BREEDING IN THE TROPICS. III. EXPERIMENTS WITH MAIZE. Ann. Roy. Bot. Gard. Peradeniya 3: [95]-184, illus.
(37) MCROSTIE, G. P.
1919. INHERITANCE OF ANTHRACNOSE RESISTANCE AS INDICATED BY A CROSS BETWEEN A RESISTANT AND A SUSCEPTIBLE BEAN. Phytopathology 9: [141]-148.
(38) ———
1921. INHERITANCE OF DISEASE RESISTANCE IN THE COMMON BEAN. Jour. Amer. Soc. Agron. 13: 15-32.
(39) MATSUURA, H.
1933. A BIBLIOGRAPHICAL MONOGRAPH ON PLANT GENETICS (GENIC ANALYSIS) 1900-1929. Ed. 2, rev. and enl., 787 pp. Sapporo, Japan.
(40) MENDEL, G.
1866. VERSUCHE ÜBER PFLANZEN-HYBRIDEN. Verhandl. Naturf. Ver. Brünn 4 (Abhandl.): 3-47.
(41) MIYAKE, K., IMAI, Y., and TABUCHI, K.
1930. CONTRIBUTIONS TO THE GENETICS OF PHASEOLUS VULGARIS. Jour. Col. Agr. Imp. Univ. Tokyo 11: 1-20, illus.
(42) NILSSON, E.
1929. ERBLICHKEITSVERSUCHE MIT PISUM. I. UNTERDRÜCKUNG DER DOMINANZ EINES FAKTORS DURCH DIE WIRKUNG ANDERER GENETISCHER FAKTOREN. Hereditas 12: [17]-32, illus.
(43) ———
1929. EINE EINFAKTORIELLE REZESSIVABWEICHUNG IN BEZUG AUF DIE FARBE DER SAMENSCHALE BEI PHASEOLUS. Hereditas 12: [41]-52, illus.
(44) ———
1929. ERBLICHKEITSVERSUCHE MIT PISUM. II. DIE VERERBUNG DER REZESSIV GELBEN KOTYLEDONENFARBE SOWIE EINIGE NEBENSRESULTATE. Hereditas 12: [223]-268.
(45) NORTON, J. B.
1915. INHERITANCE OF HABIT IN THE COMMON BEAN. Amer. Nat. 49: 547-561.
(46) PARKER, M. C.
1934. INHERITANCE OF A LEAF VARIEGATION IN THE COMMON BEAN. Jour. Heredity 25: 165-170, illus.
(47) ———
1936. INHERITANCE OF RESISTANCE TO THE COMMON MOSAIC VIRUS IN THE BEAN. Jour. Agr. Research 52: 895-915, illus.
(48) PELLEW, C.
1928. FURTHER DATA ON THE GENETICS OF "ROGUES" AMONG CULINARY PEAS (PISUM SATIVUM). 5th Internatl. Kong. Vererbungswiss., Berlin, 1927, Verhandl. 2: [1157]-1181, illus.
(49) ——— and SVERDRUP, A.
1923. NEW OBSERVATIONS ON THE GENETICS OF PEAS (PISUM SATIVUM). Jour. Genetics 13: [125]-131, illus.

(50) PICKERING, C.
1879. CHRONOLOGICAL HISTORY OF PLANTS; MAN'S RECORD OF HIS OWN EXISTENCE ILLUSTRATED THROUGH THEIR NAMES, USES, AND COMPANIONSHIP. 1222 pp., illus. Boston.
(51) PIERCE, W. H.
1934. VIROSES OF THE BEAN. Phytopathology 24: 87–115, illus.
(52) ———
1935. THE INHERITANCE OF RESISTANCE TO COMMON BEAN MOSAIC IN FIELD AND GARDEN BEANS. Phytopathology 25: 875–883, illus.
(53) PRAKKEN, R.
1934. INHERITANCE OF COLOURS AND POD CHARACTERS IN PHASEOLUS VULGARIS L. Genetica [The Hague] 16: [177]–294, illus.
(54) RANDS, R. D., and BROTHERTON, W., JR.
1925. BEAN VARIETAL TESTS FOR DISEASE RESISTANCE. Jour. Agr. Research 31: 101–154, illus.
(55) RASMUSSON, J.
1927. GENETICALLY CHANGED LINKAGE VALUES IN PISUM. Hereditas 10: 1–152, illus.
(56) ———
1933. A CONTRIBUTION TO THE THEORY OF QUANTITATIVE CHARACTER INHERITANCE. Hereditas 18: [245]–261, illus.
(57) ———
1934. GENETICALLY CHANGED LINKAGE VALUES IN PISUM. II. SEGREGATION OF LINKAGE INTENSITY IN CROSSES. Hereditas 19: [323]–340.
(58) ———
1935. STUDIES ON THE INHERITANCE OF QUANTITATIVE CHARACTERS IN PISUM. I. PRELIMINARY NOTE ON THE GENETICS OF FLOWERING. Hereditas 20: [161]–180.
(59) RHIND, D.
1933. A NOTE ON THE INHERITANCE OF SEED COAT COLOUR IN PHASEOLUS LUNATUS L. Indian Jour. Agr. Sci. 3: 360–364, illus.
(60) SAX, K.
1923. THE ASSOCIATION OF SIZE DIFFERENCES WITH SEED-COAT PATTERN AND PIGMENTATION IN PHASEOLUS VULGARIS. Genetics 8: 552–560.
(61) ———
1924. THE NATURE OF SIZE INHERITANCE. Natl. Acad. Sci. Proc. 10: 224–227.
(62) ———
1926. A GENETICAL INTERPRETATION OF ECOLOGICAL ADAPTATION. Bot. Gaz. 82: 223–227.
(63) ———
1926. QUANTITATIVE INHERITANCE IN PHASEOLUS. Jour. Agr. Research 33: 349–354.
(64) SCHREIBER, F.
1932. RESISTENZZÜCHTUNG BEI PHASEOLUS VULGARIS. Phytopath. Ztschr. 4: [415]–454.
(65) ———
1934. ZUR GENETIK DER WEISSEN SAMENFARBE BEI PHASEOLUS VULGARIS. Zuchter 6: 53–61, illus.
(66) SHAW, J. K.
1913. THE INHERITANCE OF BLOSSOM COLOR IN BEANS. Mass. Agr. Expt. Sta. Ann. Rept. 25: 182–203, illus.
(67) ——— and NORTON, J. B.
1918. THE INHERITANCE OF SEED COAT COLOR IN GARDEN BEANS. Mass. Agr. Expt. Sta. Bull. 185, pp. [59]–104.
(68) SIRKS, M. J.
1922. THE COLOURFACTORS OF THE SEEDCOAT IN PHASEOLUS VULGARIS L. AND IN PH. MULTIFLORUS WILLD. Genetica [The Hague] 4: [97]–138, illus.
(69) SUTTON, E.
1935. HALF-DISJUNCTION IN AN ASSOCIATION OF FOUR CHROMOSOMES IN PISUM SATIVUM. Ann. Bot. [London] 49: [689]–697, illus.

(70) SVERDRUP, A.
1927. LINKAGE AND INDEPENDENT INHERITANCE IN PISUM SATIVUM. Jour. Genetics 17: [221]-251, illus.
(71) TAVČAR, A.
1926. DIE VERERBUNG DER ANZAHL VON SPALTOFFNUNGEN BEI PISUM SATIVUM L. Ztschr. Pflanzenzücht. 11: 241-259.
(72) TEDIN, H., and TEDIN, O.
1926. CONTRIBUTIONS TO THE GENETICS OF PISUM. IV: LEAF AXIL COLOUR AND GREY SPOTTING OF THE LEAVES. Hereditas 7: [102]-108, illus.
(73) ——— and TEDIN, O.
1928. CONTRIBUTIONS TO THE GENETICS OF PISUM. V: SEED COAT COLOUR, LINKAGE AND FREE COMBINATION. Hereditas 11: 1-62, illus.
(74) TJEBBES, K.
1927. DIE SAMENFARBEN IN KREUZUNGEN VON PHASEOLUS VULGARIS × MULTIFLORUS. Hereditas 9: [199-208].
(75) ———
1931. TWO LINKAGE GROUPS IN THE GARDEN BEAN. Hereditas 15: [185]-193.
(76) ——— and KOOIMAN, H. N.
1921-22. ERFELIJKHEIDSONDERZOEKINGEN BIJ BOONEN. IV-VIII. Genetica [The Hague] 3: [28]-49, 1921; 4: [447]-456, illus, 1922.
(77) TRACY, W. W., JR.
1907. AMERICAN VARIETIES OF GARDEN BEANS. U. S. Dept. Agr., Bur. Plant Indus. Bull. 109, 173 pp., illus.
(78) TSCHERMAK, E.
1912. BASTARDIE RUNGSVERSUCHE AN LEVKOGEN, ERBSEN UND BOHNEN MIT RÜCKSICHT AUF DIE FAKTORENLEHRE. Ztschr. Induktive Abstam. u. Vererbungslehre 7: 81-234.
(79) ———
1916. ÜBER DEN GEGENWÄRTIGEN STAND DER GEMÜSEZÜCHTUNG. Ztschr. Pflanzenzücht. 4: [65]-104.
(80) VAVILOV, N. I.
1926. STUDIES ON THE ORIGIN OF CULTIVATED PLANTS. Trudy Prikl. Bot., Genetike i Selek. (Bull. Appl. Bot., Genetics and Plant Breeding) 16, no. 2, 248 pp., illus. [In Russian. English summary, pp. 139-248.]
(81) ———
1935. [BOTANICAL-GEOGRAPHICAL BASIS OF SELECTION.] 60 pp. Moskva and Leningrad. [In Russian. An abridged transl. in French in Rev. Appl. Bot. 16: 124-129, 214-223, 285-293. 1936.]
(82) WADE, B. L.
1929. INHERITANCE OF FUSARIUM WILT RESISTANCE IN CANNING PEAS. Wis. Agr. Expt. Sta. Research Bull. 97, 32 pp., illus.
(83) WEINSTEIN, A. I.
1926. CYTOLOGICAL STUDIES ON PHASEOLUS VULGARIS. Amer. Jour. Bot. 13: 248-265, illus.
(84) WELLENSIEK, S. I.
1922. DE ERFELIJKHEID VAN HET AL OF NIET BEZIT VAN "DRAAD" BIJ RASSEN VAN PHASEOLUS VULGARIS L. (HEREDITY OF STRINGINESS OF PHASEOLUS VULGARIS L. VARIETIES). Genetica [The Hague] 4: [443]-446.
(85) ———
1925. GENETIC MONOGRAPH ON PISUM. Bibliog. Genetica 2: [343]-476, illus.
(86) ———
1925-28. PISUM-CROSSES. I-III. Genetica [The Hague] 7: 2-64, [337]-364, illus., 1925; 11: [225]-256, 1928.
(87) ———
1927-30. LINKAGE-STUDIES IN PISUM. I-III. Genetica [The Hague] 9: [443]-466, 1927; 11: [273]-292, 1929; 12: 1-32, 1930.
(88) ———
1928. PISUM-CROSSES. IV: THE GENETICS OF WAX. Meded. Landbouwhoogesch. [Wageningen] 32, no. 9, 27 pp.

138904°—37——19

(89) WELLENSIEK, S. I.
1929. THE OCCURRENCE OF MORE THAN 50% CROSSING-OVER IN PISUM. Genetica [The Hague] 11: [509]–518.
(90) ——— and KEYSER, J. S.
1929. PISUM-CROSSES. V: INHERITED ABORTION AND ITS LINKAGE-RELATIONS. Genetica [The Hague] 11: [329]–334, illus.
(91) WHITE, O. E.
1917. INHERITANCE STUDIES IN PISUM. IV. Jour Agr. Research 11: 167–190.
(92) WINGE, O.
1936. LINKAGE IN PISUM. Compt. Rend. Lab. Carlsberg Sér. Phys. 21: 271–293.
(93) WINTON, D. DE
1928. FURTHER LINKAGE WORK IN PISUM SATIVUM AND PRIMULA SINENSIS. 5th Internatl. Kong. Vererbungswiss., Berlin, 1927, Verhandl. 2: [1594]–1600.
(94) WÓYCICKI, S.
1927. GENETISCHE STUDIEN ÜBER DIE HÜLSENFORMEN BEI DEN BOHNEN. Acta Soc. Bot. Polon. 5: [20]–51, illus. [In Polish. German summary, pp. 48–51.]
(95) ZAUMEYER, W. J., and WADE, B. L.
1935. THE RELATIONSHIP OF CERTAIN LEGUME MOSAICS TO BEAN. Jour. Agr. Research 51: 715–749, illus.
(96) ——— and WADE, B. L.
1936. PEA MOSAIC AND ITS RELATION TO OTHER LEGUME MOSAIC VIRUSES. Jour. Agr. Research 53: 161–185, illus.